SPORES WITH BIFURCATE PROCESSES FROM THE MIDDLE OLD RED SANDSTONE OF SCOTLAND

by J. B. RICHARDSON

ABSTRACT. Plant spores are described from Middle Old Red Sandstone deposits of the Orcadian basin, Scotland. The genus *Ancyrospora* Richardson 1960 is reinterpreted. The species *Hystricosporites corystus*, *Perotrilites bifurcatus*, *Ancyrospora longispinosa* are new. In addition the most numerous spores are included in the species *Ancyrospora ancyrea* (Eisenack) comb. nov. which is subdivided into the varieties *A. ancyrea* var. *ancyrea* var. nov., *A. ancyrea* var. *brevispinosa* var. nov., and *A. ancyrea* var. *spinobaculata* var. nov. The range of variation of *A. ancyrea* is described in detail and compared at two different horizons. Finally the local and regional stratigraphic distribution of all these spores is discussed and their relative importance assessed. A new generic name *Calyptosporites* is proposed, in place of *Cosmosporites* Richardson (preoccupied).

LANG (1925) discovered in the Cromarty nodule beds a group of spores with anchor-shaped appendages, which he designated type G. Since then numerous authors have described spores with similar appendages and referred them to this type. Although this distinctive ornamentation is similar in each case it occurs on spores of various structural organizations, e.g. azonate, zonate, cingulate, and monosaccate.

Spores with bifurcate processes are characteristic of Middle and Upper Devonian deposits of many areas in the northern hemisphere, Canada, U.S.A., Scotland, Spitsbergen, France, Germany, and the U.S.S.R. They have also been described by Luber (1955) from basal Carboniferous deposits which increases the likelihood that they will be found in other Lower Carboniferous strata. This morphological feature is nevertheless highly characteristic of Middle and Upper Devonian strata (see text-fig. 15) and Luber (1955) while recording an azonate spore with bifurcate appendages from C_1 (Strunian) of Western Kazakhstan commented that this spore species was especially characteristic of the Upper Devonian of both the European and Asiatic parts of the U.S.S.R.

So far no reports of Middle Devonian spores (Radforth and McGregor 1954, 1956) bearing these appendages have been made from Canada although they have been recorded by various authors from the Upper Devonian. This may be due to the fact that the age of the described deposits may not be Middle Devonian; alternatively if these deposits are accurately dated, spores with bifurcate appendages may have appeared later in North America than in Europe. Spore assemblages from more accurately dated samples of Middle Devonian age are needed before detailed comparisons can be made.

The European Middle Devonian strata are closely comparable; similar assemblages to those in Scotland have been described by Eisenack 1944 (Baltic Germany), Hoeg 1942 (Spitsbergen), and especially Kedo 1955, 1957 (Belorussiya). Kedo in a personal communication says 'the Middle Givetian of Belorussiya contains large amounts of all forms of the spores you describe' (i.e. Richardson 1960), and considers that the Middle Devonian of Belorussiya and of Scotland belong to a single floristic region. Also Naumova (1953) and Tchibrikova (1959) have described spores with bifurcate appendages

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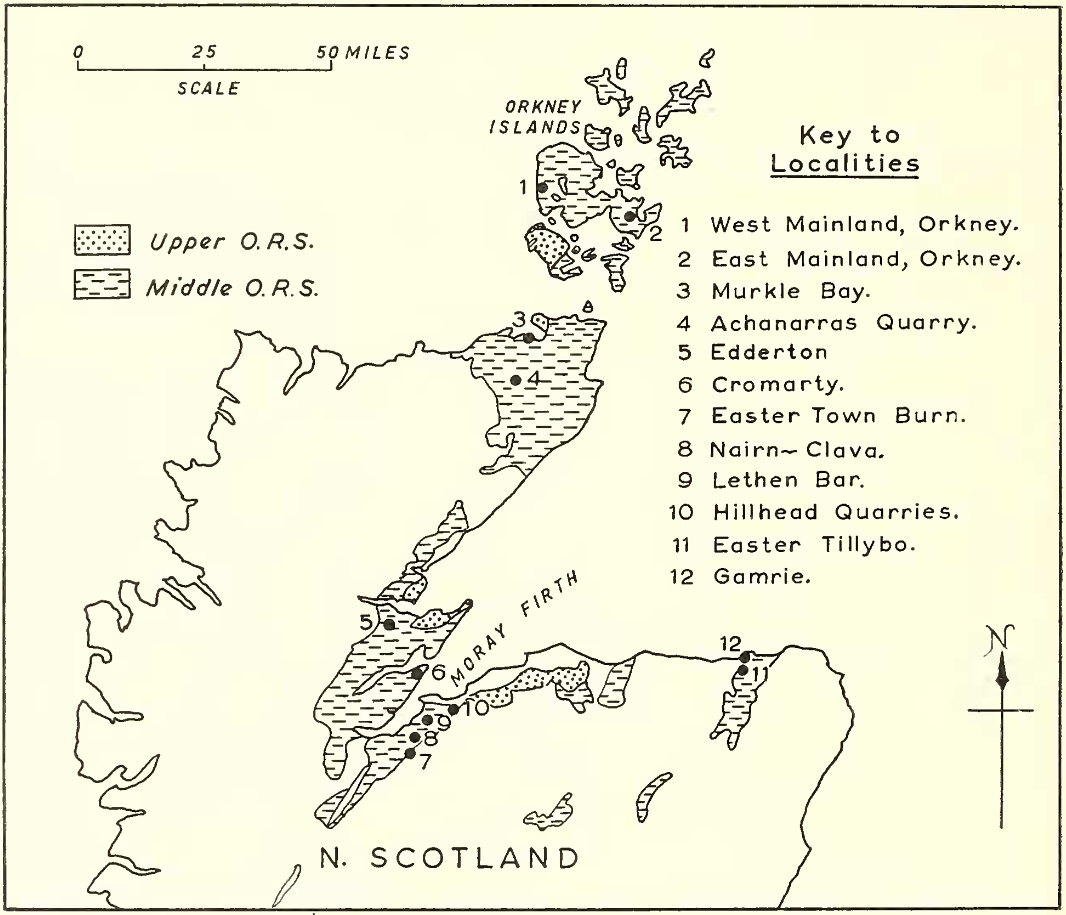
from Middle and Upper Devonian deposits of Russia many of which appear identical to the forms described here.

The present paper describes spores arbitrarily referred to as type G from various strata throughout the Orcadian basin (north-east Scotland) including Lang's localities



TEXT-FIG. 1. Index map of localities and distribution of the Old Red Sandstone, Orcadian basin. Numbers refer to sampling areas.

in the neighbourhood of Cromarty. In addition other spores with these distinctive appendages are also described which have not previously been recorded from this area. The wide range of variation of some of these spores, which often form as much as 50 per cent. of the total spore assemblage, is described and their stratigraphic distribution discussed.

Acknowledgements. The author wishes to express his sincere gratitude to Professor L. R. Moore for constant advice and encouragement during the work and for helpful suggestions in the preparation of the manuscript, and to Dr. R. Neves and Dr. J. E. Prentice who have read the manuscript and made several useful suggestions. Thanks are due also to Mr. E. O. Rowland for technical assistance, Miss M. Shaw for help in producing the plates, and to Mr. A. Atkins for valuable assistance with the text-figures.

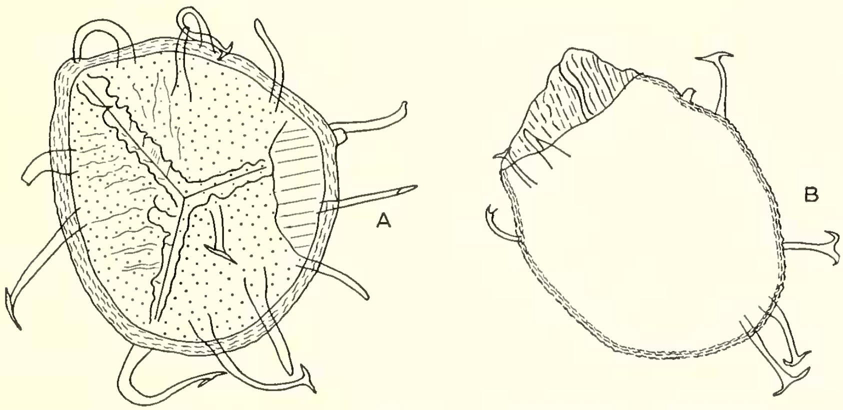
Classification

Most of the spores recorded can be fitted into the existing classification of Potonié and Kremp (1954). The genus *Ancyrospora* Richardson 1960 is, however, difficult to assign. Spores included in this genus have two distinct membranes the outer one of which is extended laterally to a variable extent in the form of a flange or pseudoflange.

This circumscription excludes the genus *Ancyrospora* from the existing supra-generic categories.

SYSTEMATIC DESCRIPTIONS

All the slides referred to by serial numbers are in the collection of the Geology Department, University of Sheffield; position on the slide is indicated by the instrument settings of a Cooke, Troughton and Simms microscope. At least twenty-five spores have been measured for each species or variety.



TEXT-FIG 2. *Hystricosporites corystus* sp. nov. A, Polar view. B, Lateral view.

Anteturma SPORITES H. Potonié 1893
Turma TRILETES Reinsch 1881
Subturma AZONOTRILETES Luber 1935
Infraturma APICULATI (Bennie and Kidston) Potonié 1956
Genus HYSTRICOSPORITES McGregor 1960

Hystricosporites corystus sp. nov.

Plate 25, figs. 1, 2; text-fig. 2

Holotype. Size 156μ (excluding spines), spines 56 to 66μ; number around the periphery 5. Slide OR 31, ref. 150543. Upper Rousay beds, East Mainland, Orkney.

Occurrence. As above.

Diagnosis. Thick-walled spores with long, parallel-sided or slightly tapering spines which widen at their apex to a pronounced bifurcation. Lips of triradiate mark greatly elevated in the form of an apical prominence.

Description. Colour reddish-brown. Size range 129 to 213μ (excluding spines). Equatorial outline subcircular to subtriangular; in lateral view subcircular with flattened apex bearing a distinct apical prominence. Spore coat consists of two closely adhering layers. Spines borne on equatorial margin and distal surface; have long parallel-sided or slightly tapered stems which only widen slightly at their base and widen near the apex to a well-marked bifurcation. Spines 26 to 66 μ long, 5 to 10 around the equatorial margin. Triradiate mark with greatly elevated, membraneous ridges (31 to 67 μ high in lateral view) which reach the equatorial margin.

Remarks. Similar spores (Plate 25, fig. 3) are found in the Lower Stromness beds, Orkney, and the Sandwick–Achanarras fish beds, Orkney and Caithness. They differ from *H. corystus* sp. nov. in the larger number of spines around the equator, also their size range 140–260 μ (excluding spines) and length of spines 39–82 μ is slightly greater. These spores have not been separated as a new species because preservation is too poor to make detailed comparisons and there is overlap between the two groups. The larger spores are referred to as *H. ?corystus* in the text.

Comparison. None of the spores figured by Eisenack (1944) resembles spores of *H. corystus* in polar view, although two of the spores figured in lateral view (Eisenack, pl. 3, figs. 4, 5) appear to be closely similar. The spores compressed in polar view, figured by Eisenack, have a variably extended outer layer and a distinct triangular 'central body' and such spores are here placed in the genus *Ancyrospora*.

H. delectabilis McGregor may have folds along the tetrad rays but these do not appear to be greatly elevated. *Nikitinsporites canadensis* Chaloner (1959) is much larger and has appendages which taper sharply at their apex (text-fig. 8).

Derivation of name. Gr. *Korystos*—crested.

Infraturma PERINOTRILITES Erdtman 1947

Genus PEROTRILITES Couper 1953

Remarks. The spores described below appear to be identical in general form to those of the genus *Perotrilites* Couper 1953. Couper's genus has a membraneous perispore. The outer membrane of *P. bifurcatus* is very delicate, transparent, and shows no infrastructure. This membrane is quite distinct from the thick, finely wrinkled exoexine of *Ancyrospora*. The term perispore is used here in the sense of Potonié and Kremp 1955.

Perotrilites bifurcatus sp. nov.

Plate 25, figs. 4, 5; text-fig. 3

EXPLANATION OF PLATE 25

All magnifications $\times 300$.

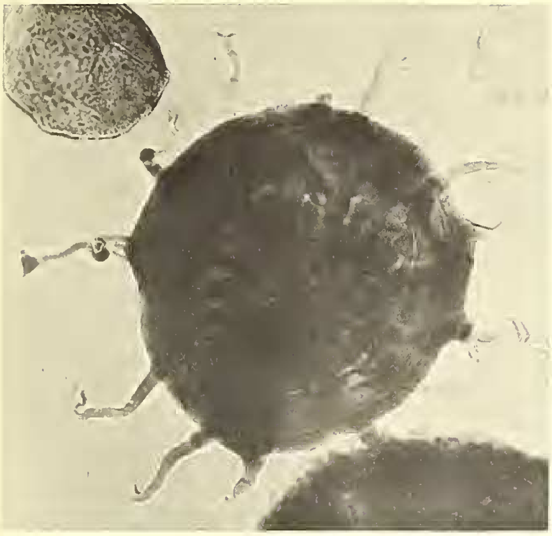
Figs. 1, 2. *Hystricosporites corystus* sp. nov. 1, Holotype. 2, Lateral view showing apical prominence. Upper Rousay beds.

Fig. 3. *Hystricosporites ?corystus* sp. nov. Sandwick fish bed.

Figs. 4, 5. *Perotrilites bifurcatus* sp. nov. 4, Holotype. 5, Oblique compression showing eccentric spore body. Coal Heugh shales.

Figs. 6, 7. *Ancyrospora ancyrea* var. *ancyrea* (var. nov.). 6, Form with moderately wide flange. 7, Spore with a wider flange. Coal Heugh shales.

Fig. 8. *A. ancyrea* var. *brevispinosa* var. nov. holotype. Coal Heugh shales.



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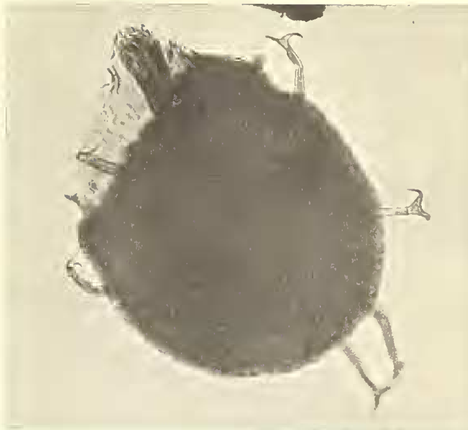

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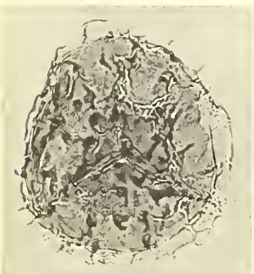

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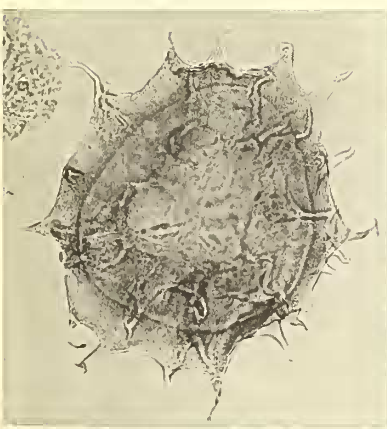

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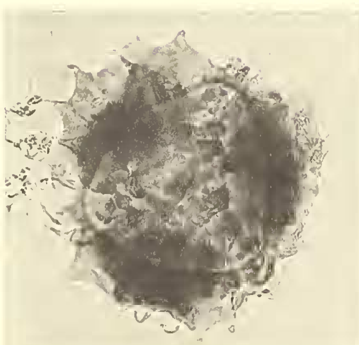

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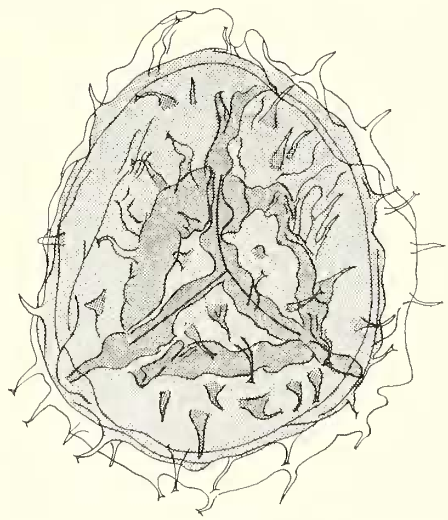
RICHARDSON, Devonian spores

Holotype. Size 88μ, body 82μ, spines 8μ long. Slide CR 171, ref. 119500. Coal Heugh shales, nodule beds, Cromarty (see Richardson 1960).

Occurrence. Lower Stromness beds, W. Mainland, Orkney; Basal beds, Easter Town burn; Basal beds, Millers Bay and nodule beds, Cromarty.

Diagnosis. Equatorial outline subcircular to elliptical, perispore thin; body thick-walled, distinct. Perispore bears small spinose processes which bifurcate at their tips.



TEXT-FIG. 3. *Perotrilites bifurcatus* sp. nov. holotype. Camera lucida drawing ×600.

Description. Colour, perispore pale yellow, body yellow to brown. Size range 80 to 103μ, body 72 to 90μ. Equatorial outline subcircular, body rounded to rounded triangular. Perispore thin, delicate, transparent, often wrinkled and contorted; not much greater than the body in diameter. Central body completely enclosed by perispore, attached by the proximal surface only; width of perispore around the body equal to subequal; occasionally body eccentrically placed. Central body distinct, smooth. Perispore ornamented by small spines with slender stems, spines widen at their bases and bifurcate at their tips; spines occur on the equatorial margin and distal surface, 5–8μ long, 6 to 11 around the periphery. Perisporal membrane often formed into contorted folds along the triradiate mark; folds may reach the equatorial margin. Also the perispore is often crumpled into arcuate folds in the interradial area. Triradiate mark simple, rays equal to $\frac{1}{2}$ radius of the body, or slightly more.

Comparison. This species closely resembles *Perotrilites sp.* McGregor 1960; both have a thin flimsy perispore bearing external ornament but differ in the kind of ornamentation. *Perotrilites sp.* McGregor has grana whereas the spores described here all bear bifurcate processes.

INCERTAE SEDIS

Genus ANCYROSPORA Richardson 1960 emend.

Plate 27, figs. 3–5; text-fig. 4

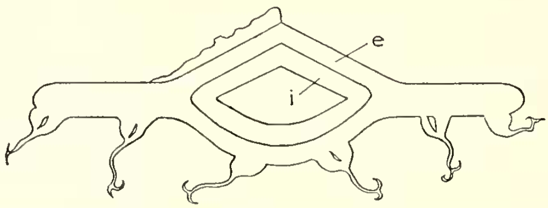
Type species. A. grandispinosa Richardson 1960.

Emended diagnosis. Radial, trilete spores, exoexine extends at the equatorial margin as a thick flange or a pseudoflange. Equatorial outline circular, subcircular, triangular, subtriangular, to scalloped and irregular. Exoexine bears spinose processes which bifurcate at their tips. Intexine of variable thickness.

Comparison. Archaeotriletes (Naum.) Potonié 1958 has a thin membraneous zona, the spinose processes are club-shaped and arise from the central area (Naumova 1953, pl. 6, fig. 2); in contrast the flange of *Ancyrospora* is thick, the spines are clearly anchor-shaped and arise all over the distal surface and the equatorial margin. In the forms with a pseudo-flange the spines form an intimate part of the equatorial rim (Plate 25, figs. 6, 7). The spores of *Nikitinsporites* Chaloner 1959 are of large size, azonate, and have distinctive spines (text-fig. 10D). *Hystricosporites* McGregor 1960 is azonate.

Remarks. The thin section (Plate 27, fig. 4) shows that although *Ancyrospora grandispinosa* Richardson 1960 consists of two thick membranes there is no cavity between the two layers (see also Plate 27, fig. 5). Consequently the original reconstruction (1960, text-fig. 6C) is incorrect and a new construction has been drawn based on a series of thin sections (text-fig. 4).

The spores of *A. ancyrea* (Eisenack) comb. nov. show a great deal of variation. In



TEXT-FIG. 4. *Ancyrospora grandispinosa*. Diagrammatic reconstruction in polar section; *e*, exoexine; *i*, intexine.

polar view they show a variably extended equatorial zone (pseudoflange). The thickness of the exoexine, size of the ridges (muri) connecting the spines, and to a lesser extent the size of the spines determine the width of the pseudoflange around the equator. In the author's opinion the variation, seen in spores (in polar compression) figured by Eisenack (pl. 1, figs. 6–8, pl. 2, fig. 2, and pl. 3, 2–3) and in the spore assemblages in the Orcadian basin, is due to the relative development of these three features.

The author agrees with Potonié 1956, Chaloner 1959, and McGregor 1960 that the genus *Archaeotriletes* (*sensu* Naumova 1953) is heterogeneous and requires some subdivision. On the other hand it is considered to be more practical to have a wide circumscription for the genus *Ancyrospora* because of the range of variation exhibited by these spores. Consequently spores with a flange (*A. grandispinosa*) and others with a pseudoflange (*A. ancyrea* (Eisenack) and *A. longispinosa* sp. nov.) are here placed in the same genus. This circumscription strictly excludes *Ancyrospora* from Turma Zonotriletes Potonié 1956 and therefore this genus is placed in *Incertae sedis*.

Many spores described in the literature appear to have a similar structure to *A. ancyrea* (Eisenack) and are listed below.

Ancyrospora (*Triletes*) *ancyrea* (Eisenack) comb. nov.

Holotype. Eisenack 1944, pl. 2, fig. 2. Size 124μ (excluding spines), 'central body' 104μ, spines 52μ long. Probably Middle Devonian.

Emended diagnosis. Exoexine variably extended in polar compression in the form of a flange; equatorial outline subcircular, subtriangular to scalloped and irregular, 'central body' distinctly subtriangular or triangular with rounded apices and convex or straight sides; spinose or spinobaculate processes which bifurcate at their tips; triradiate mark usually accompanied by folds which may be elevated as an apical prominence.

Comparison. The spores described by Eisenack (1944) have a marked apical prominence. Many of the Orcadian spores have folds along the tetrad rays which in some forms are elevated to form small apical ridges. These are not as prominent as those illustrated by Eisenack. However, this is regarded as insufficient justification for erecting a new species especially since the other major features such as the dominantly subtriangular outline, the distinct subtriangular 'central body', the nature and distribution of the spines, and the variable extension of the exoexine appear to be identical in both cases. The only differences appear to be the greater development of an apical prominence in the case of the Baltic spores and the spinobaculate and small forms with a narrow pseudoflange from the Orcadian deposits. Consequently the main complex of spores of type G2 Lang is grouped with *Triletes ancyreus* Eisenack and the variations in the Orcadian spores referred to above are separated as varieties.

A. ancyrea Eisenack comb. nov. differs from *A. grandispinosa* Richardson 1960 in having a subtriangular to irregular outline, a marked subtriangular 'central body', and a variably extended pseudoflange.

List of probable synonymy

Archaeotriletes gibbosus Naumova 1953 (80–85μ) closely resembles some of the types with a narrow 'flange'.

'*Grandispora*' Hoffmeister, Staplin, and Malloy 1955 (pl. 1, fig. 10) appears very similar to *An. ancyrea* although smaller and with a more incised margin; size 62μ (excluding spines) measured from photograph.

Archaeotriletes sincerus Kedo 1957 (78μ) has a regular border and spines clearly separated at their bases and is clearly subtriangular in outline.

Archaeotriletes hamulus Naum. var. *giganteus* Tchibrikova 1959 (80–90μ) appears double layered and has a subtriangular central area. The spore figured is closely similar to some of the Orcadian specimens of *Ancyrospora ancyrea*.

Archaeotriletes langi Taugourdeau-Lantz 1960 has a dominantly triangular outline and appears similar to *Ancyrospora ancyrea*. However, it cannot be seen whether or not a 'central body' is present. The nature of the spines appears different; in the case of *Archaeotriletes langi* they have wide conical bases which taper uniformly throughout their length in contrast to *Ancyrospora ancyrea* in which the spines have wide bases abruptly joining slender stems. Again in *Archaeotriletes langi* the margin is much more incised.

Ancyrospora ancyrea var. *ancyrea* var. nov.

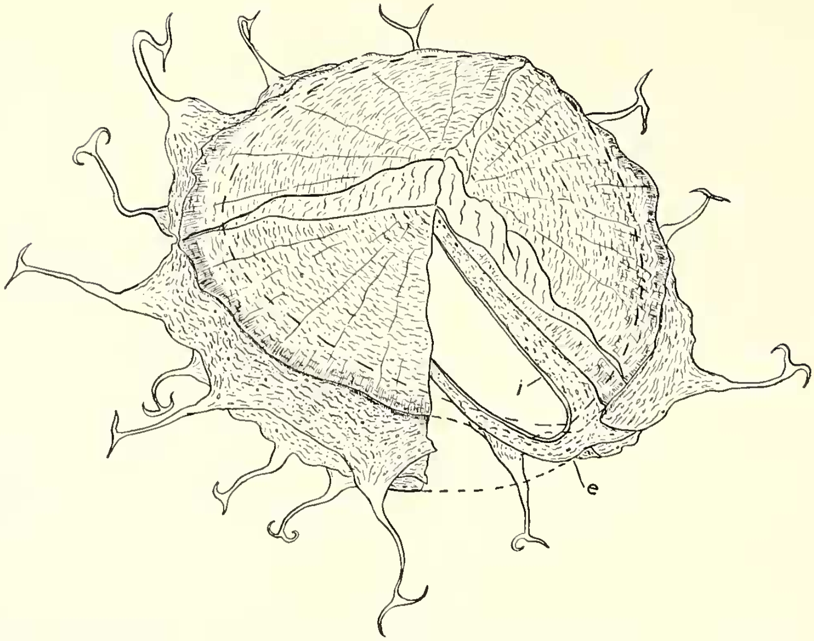
Plate 25, figs. 6, 7; text-figs. 5, 6, 10B

1925 Type G2 Lang, p. 257, pl. 1, figs. 16, 17.
1944 *Triletes ancyreus* Eisenack, p. 110 (pars), pl. 2, fig. 2, pl. 1, figs. 7, 8.

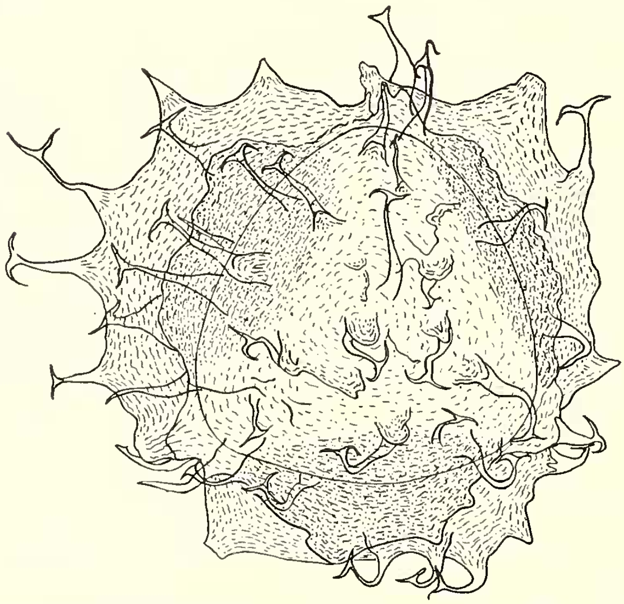
Holotype. Same as species *ancyrea*.

Occurrence. Found in beds throughout the area rare in the Upper Rousay beds.

Diagnosis. Exoexine moderately to distinctly extended in polar compression; spinose



TEXT-FIG. 5. Hypothetical reconstruction of *Ancyrospora ancyrea* (Eisenack) comb. nov.; *e*, exoexine; *i*, intexine.



TEXT-FIG. 6. *Ancyrospora ancyrea* var. *ancyrea* var. nov. Specimen with wide pseudoflange in the interradial areas. Camera lucida drawing ×600.

processes have wide bases, slender stems and bifurcate tips; triradiate mark distinct, $\frac{1}{3}$ to $\frac{1}{2}$ radius of the body.

Description. Colour yellow to dark brown. Size range (excluding spines) 82 to 169μ, 'central body' 51 to 116μ. Pseudoflange width around the 'central body' equal to subequal in proximal view; surface of exoexine covered with numerous minute wrinkles, infrapunctate or occasionally infragranular; 'central body' smooth. Exoexine bears spinose processes on distal surface and equatorial margin 8 to 51μ long, which have wide conical bases, more slender stems, and a well-marked bifurcation at their tips; adjacent spines are often joined at their bases by folds of the exoexine (text-fig. 10), occur in more or less concentric rows and occasionally are interconnected giving an irregular reticulate pattern. Number of spines around the equator 11 to 13. Triradiate mark distinct, spore coat occasionally splayed open along rays, rays $\frac{1}{3}$ to $\frac{1}{2}$ the radius of the body; on some specimens there are contorted folds along the tetrad rays which may be elevated to form an apical prominence.

Ancyrospora ancyrea var. *brevispinosa* var. nov.

Plate 25, fig. 8; text-fig. 9A

Holotype. Size 93μ, central body 80μ, spines 8 to 13μ long, number around the equator 15; slide CR 170, ref. 103490. Coal Heugh shales.

Occurrence. Found in all beds throughout the area; rare in all samples except the Upper Rousay beds, and Eday beds, East Mainland, Orkney.

Diagnosis. Exoexine only slightly extended with regular subtriangular outline, bears small discrete spines which bifurcate at their tips.

Description. Colour yellow to dark brown. Size range, excluding spines, 75 to 106μ, 'central body' 62 to 93μ. Equatorial 'body' outline subtriangular. Pseudoflange width around the 'central body' equal to subequal in proximal view; surface of the exoexine covered by numerous minute wrinkles, infrapunctate; 'central body' smooth. Exoexine bears short spines with wide, hollow bases, slender stems, and bifurcate tips. Spines distinct and separate occur on the distal surface and equatorial margin; spine length 5 to 13μ, number around the equator 10 to 15. Triradiate mark indistinct equals half spore radius; occasionally there are small contorted folds along the rays.

Remarks. There is a great variety of spine length in spores of *A. ancyrea.* Frequently large and small spines occur on the same spore. There is also variation in the extension of the flange so that there are some spores which are difficult to assign either to *A. ancyrea* var. *brevispinosa* or var. *ancyrea.* Because of this partial overlap the forms with short discrete spines and slightly extended flange are distinguished at the varietal level. They have been thus separated since typical examples of each are quite distinct and for the further reason that *A. ancyrea* var. *ancyrea* is most abundant at the Achanarras horizon whilst var. *brevispinosa* is especially abundant in the Upper Rousay beds.

Comparison. This variety resembles *A. ancyrea* var. *ancyrea* var. nov. in general organization but differs from it in having small discrete spines and an outer membrane which is only slightly extended in polar compression. Some of the spores described by Kräusel and Weyland (1929) (pl. 14, fig. 2, text-fig. 30) have short, slender spines but the spores figured are opaque so it cannot be seen whether they had a 'central body'. '*Archaeotriletes*' *hamulus* var. *famenensis* Naum. 1953 resembles var. *brevispinosa* but has a more rounded outline.

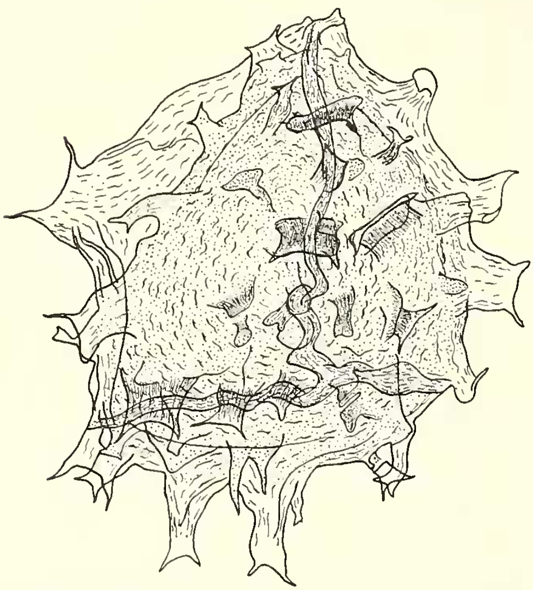
Ancyrospora ancyrea var. *spinobaculata* var. nov.

Plate 26, fig. 4; plate 27, figs. 1–2; text-figs. 7, 10A

Holotype. Size 143·8μ, 'central body' 98μ, spines 15 to 18μ long, 15 to 23μ wide. Number of spines around the equatorial margin eight. Slide CR 170, ref. 149527. Coal Heugh shales.

Occurrence. Basal flagstones, Easter Town burn; nodule beds (Achanarras horizon), Cromarty.

Diagnosis. Pseudoflange variably extended; equatorial outline subtriangular to irregular; bears wide more or less parallel-sided projections with slight increase at base and slender bifurcations at their tips.



TEXT-FIG. 7. *Ancyrospora ancyrea* var. *spinobaculata* var. nov. Camera lucida drawing ×600.

Description. Colour yellow to dark brown. Size range 88 to 154μ, 'central body' 69 to 98μ. Equatorial outline subtriangular to irregular, 'central body' subtriangular. Pseudo-flange width around the 'central body' equal to subequal in proximal view, covered with minute wrinkles; 'central body' smooth. Exoexine bears stout, more or less parallel-sided processes on the distal surface and equatorial margin. Spines have wide bases with stems only slightly less wide; they vary from forms in which the height is only slightly greater than width to others more elongated. This size variation may occur on the same spore. Number of spines around the periphery 8 to 13. Triradiate mark indistinct $\frac{1}{2}$ to $\frac{2}{3}$ body radius; occasionally there are triradiate folds which reach the periphery.

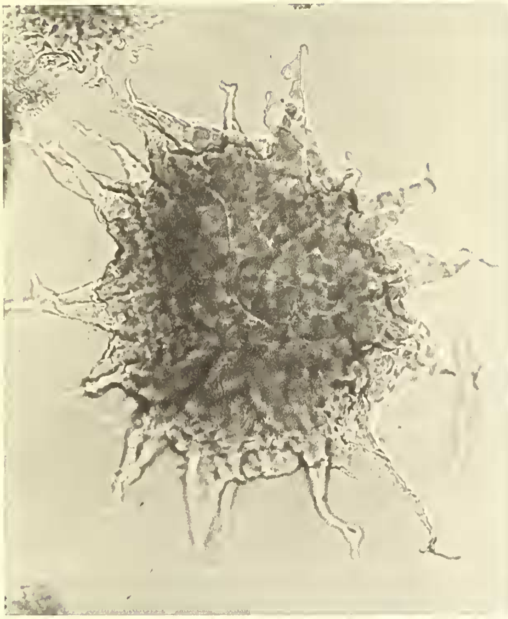
Remarks. Spores of this type from Navity shore samples often have more slender spines and greater variety of spine width on the same spore. Also several spores (Coal Heugh) show a mixture of spine types, i.e. wide, parallel-sided spines typical of var. *spinobaculata* and slender spines typical of *A. ancyrea* var. *ancyrea*.

Comparison. *A. ancyrea* var. *spinobaculata* differs from the other forms described here by having wide, parallel-sided spines. This variety resembles spores described and figured

EXPLANATION OF PLATE 26

Figs. 1–3. *Ancyrospora longispinosa* sp. nov., ×250. 1, Holotype. 2, Distal view of another specimen; Basal beds, Easter Town burn. 3, Specimen from the Lower Stromness beds, Orkney.

Fig. 4. *Ancyrospora ancyrea* var. *spinobaculata* var. nov. holotype, ×300; Coal Heugh shales.



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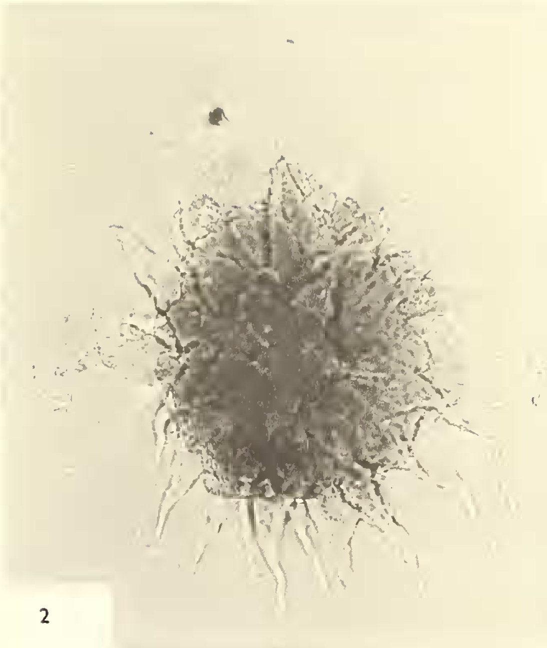

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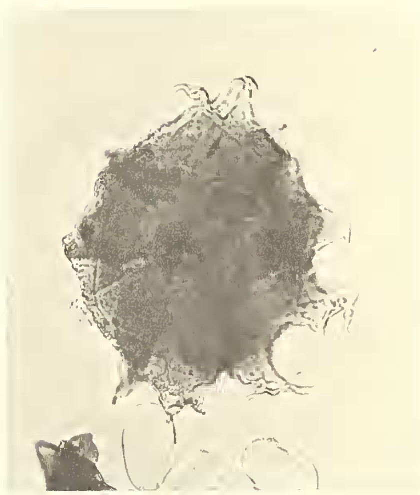

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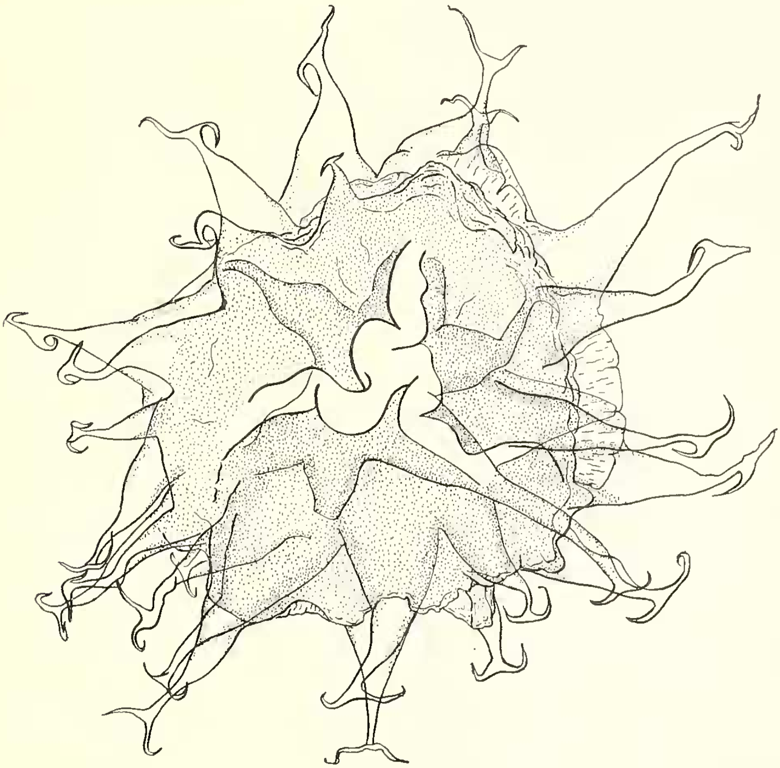
RICHARDSON, *Ancyrospora*

under the group Apiculati (Thomson) by Høeg (1942, pl. 31, figs. 17, 18). Høeg described two forms with bifurcate spines one of which had spines of greater width than the other. Although the width of the spines does not seem as great as some of those described here, Høeg's form probably belongs to this species if a 'central body' is present.

Archaeotriletes fidus Naumova 1953 also shows wide processes but these are more tapering than those of var. *spinobaculata*. Further, Naumova does not describe a 'central body' and *A. fidus* has a diameter of only 30 to 40μ.



TEXT-FIG. 8. *Ancyrospora longispinosa* sp. nov. holotype. Camera lucida drawing approximately $\times$ 400.

Ancyrospora longispinosa sp. nov.

Plate 26, figs. 1–3; text-fig. 8

Holotype. Size 190μ (excluding spines), spines 100–120μ. Slide MF 27, ref. 145550. Basal flagstones, Easter Town burn.

Occurrence. Only found in Lower Stromness beds, West Mainland, Orkney, and Basal beds, Easter Town burn.

Diagnosis. Subcircular to subtriangular spores, 'central body' indistinct; ornament consists of long bifurcate processes with wide conical bases which taper gradually for over $\frac{2}{3}$ of their length, followed by a short slender portion with long, slender bifurcations. Spines arranged in a radial manner.

Description. Colour reddish-brown. Size range 180 to 236 μ (excluding spines). Equatorial margin often appears irregular due to the wide bases of the spines but subcircular to subtriangular. 'Central body' subtriangular (not seen in all specimens due to the thick nature of the spore coat). Spore coat thick, bears long spines in concentric rows, often fused at their bases. The wide-based conical spines are distinctive; spines 70 to 120 μ long. Contorted folds occur along the tetrad rays forming elevated lips 24–48 μ high.

Comparison. This species differs from *A. ancyrea* (Eisenack) comb. nov. in the presence of long conical spines. '*Archaeotriletes langi*' Taugourdeau-Lantz also has conical spines but these are considerably shorter, about 18 μ in length, and appear more numerous.

A STUDY OF VARIATION IN THE SPECIES *ANCYROSPORA ANCYREA*

Several spore genera in the Orcadian deposits show a considerable degree of morphological variation. This is apparent even in the specimens from one sample, and is especially noticeable at the Achanarras horizon. At this stratigraphic level there are relatively few basic spore morphologies but the variation on these is considerable. Because of this, species are often difficult to delimit. In contrast the spores of the Upper Rousay beds comprise a greater number of basic types which are clearly differentiated.

Vertical changes in spore form are also apparent and, since these changes often show consistent trends, they may prove to be useful for stratigraphic correlation.

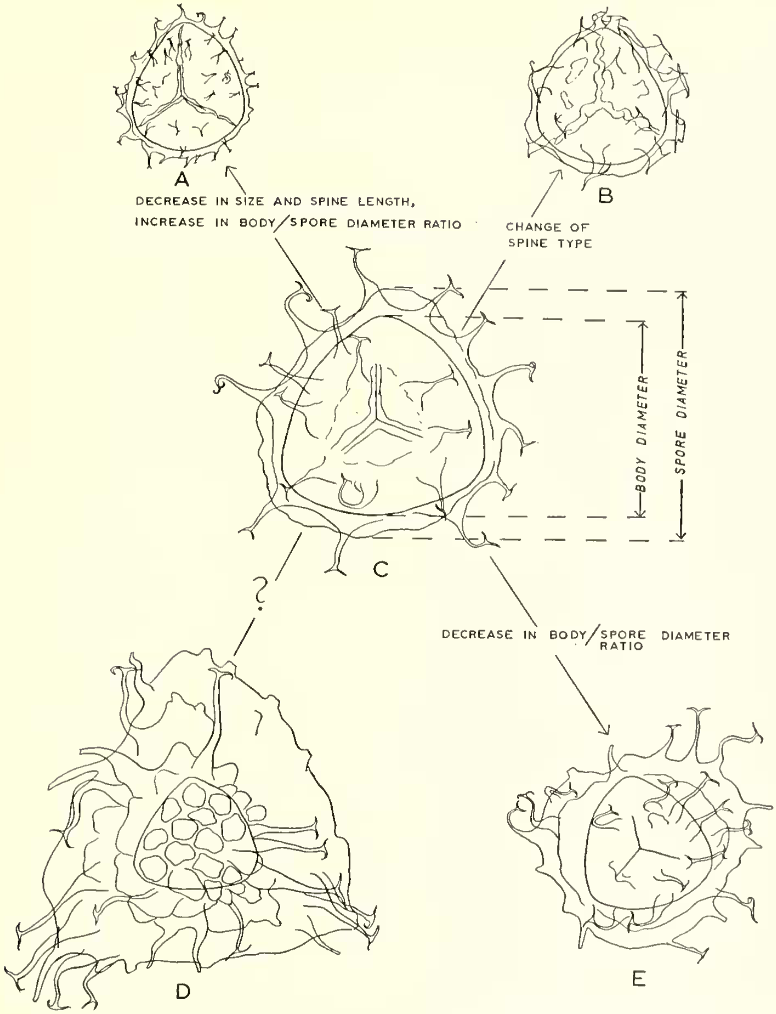
Variation observed in a single sample

Spores of the species *Ancyrospora ancyrea* from the Achanarras Horizon (text-figs. 9, 10) have a well-defined, rounded triangular 'central body', and a relatively thick exoexine which bears bifurcate processes. Apart from these features there is a considerable degree of morphological variation, in size, 'body'/spore diameter ratio, equatorial outline and length, shape, and distribution of spines.

The exoexine shows various degrees of extension in polar view. Some spores have pseudoflange which is narrow and very similar to the 'body' in equatorial outline (e.g. *Ancyrospora ancyrea* var. *brevispinosa*). Other spores show different degrees of extension of the equatorial zone, in some cases the extension is uniform and very marked (text-fig. 9D) whereas in others more pronounced distension occurs in the inter-radial areas (text-fig. 9E).

Spine variation in this species is also very striking. In the most numerous specimens the spines can be divided into three distinct parts, a wide sharply tapering basal area, a long slender stem (only slightly tapered), and a diverging part at the apex which bifurcates. The relative length of these parts varies considerably. Sometimes the basal area extends for most of the length of the spines, whereas more often a long slender stem is present. The spines of *A. ancyrea* var. *spinobaculata* are very distinctive as they are parallel sided but vary in width and length. Also the length of their bifurcations may be very small, or, alternatively, long and slender (text-fig. 10A). Intermediate forms have been found, however, which contain typical spines of *A. ancyrea* var. *ancyrea* in addition to the spines of var. *spinobaculata*.

It is the presence of these intermediate forms which has caused the author to use

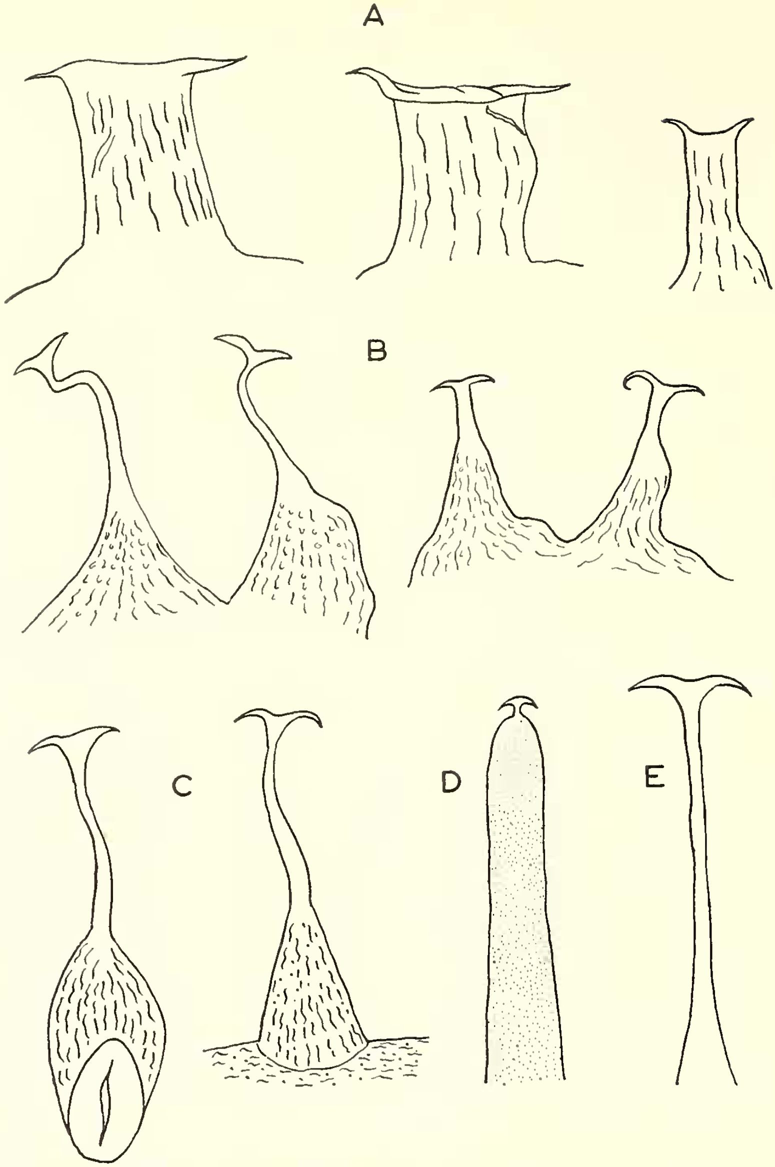


TEXT-FIG. 9. Variation of the species *Ancyrospora ancyrea* (Eisenack) comb. nov. in Coal Heugh shales. A, var. *brevispinosa* var. nov. B, var. *spinobaculata* var. nov. C, E, var. *ancyrea* var. nov. specimens with variably extended pseudoflange. D, *Ancyrosporas p.* specimen with wide equatorial zone, Navity shore shales.

a trinomial system of nomenclature in the belief that the variation of the spore complex *A. ancyrea* is most clearly represented in this way.

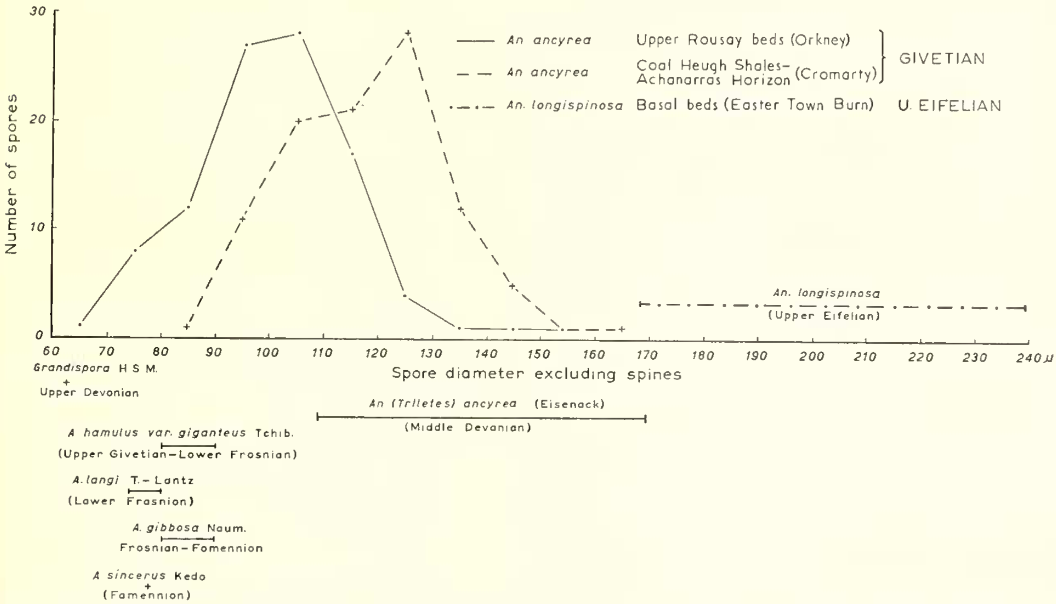
Variation in two different samples (*Coal Heugh shale and shale from the Upper Rousay Flagstone Group*)

In order to make the results directly comparable these two samples have been subjected to the same amount of maceration in Schulze solution. It is known that after treatment of the material in Schulze solution and potassium hydroxide spores swell. At the same time it is necessary to treat the spores in this manner in order to render the



TEXT-FIG. 10. Anchor-shaped appendages of various spores. A and B, spine variation in *Ancyrospora ancyrea* (Eisenack). A, var. *spinobaculata*. B, var. *ancyrea*. C, *Ancyrospora grandispinosa* Richardson 1960. D, *Nikitinsporites canadensis* Chaloner 1959. E, *Hystricosporites corystus* sp. nov.

dark-brown walls less opaque, to facilitate microscopical examination. However, detailed observations were made on preparations not treated in Schulze solution and comparisons made with part of the same material after Schulze maceration. This was done to see if any of the characters observed were artifacts due to the treatment. Forms with a variably extended pseudoflange, spinobaculate, and the other morphological types distinguished were found in both unmacerated and macerated preparations. The spore size, however, was found to increase considerably and the tetrad folds were often found to be corroded after treatment. A surprising feature was that the spine length on 100 specimens measured from one unmacerated and a macerated sample were practically identical. These observations enabled some of the limitations of the following comparisons to be ascertained.



TEXT-FIG. 11. Frequency distribution graph to show the diameter excluding spines of *Ancyrospora ancyrea* (Eisenack) comb. nov. and the size range of similar species. Based on 100 specimens of *A. ancyrea* from each sample.

Comparison of the variation in two samples. A preliminary examination of the two samples showed that larger forms with a wide pseudoflange and fairly long spines are common in the Coal Heugh sample whereas in the higher sample (Upper Rousay beds) spores typical of the variety *brevispinosa* are dominant and also the variety *spinobaculata* was absent. Comparison of the two samples in detail shows three main trends:

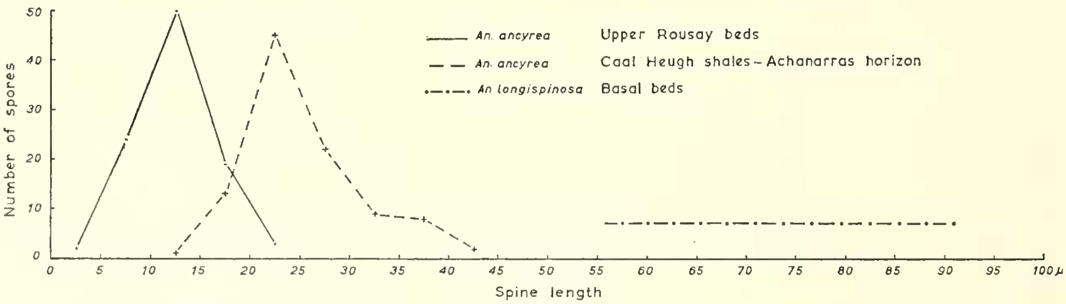
(*a*) reduction in size of spore,
(*b*) reduction in size of spines, and
(*c*) increase in 'body'/spore diameter ratio.

Reduction in the size of the spore. The graph (text-fig. 11) shows the spore size (without spines) of 100 specimens from each sample. There is a considerable degree of overlap between the two 'populations'; on the other hand the two modes appear to be distinct. The following statistical constants were calculated to test the statistical validity of these results.

't' for difference between means = 8·19 ('t' value for P = 0·01 is 3·4).
Variance ratio = 1·014 (V.R. value for P = 0·1 is 1·66).

These figures show that the difference between the means is significant and not due to random sampling of the same 'population' nor to differences in the group variances (Fisher and Yates 1948). This indicates that there is a real difference in the size of spore between the two groups.

It may still be argued that these differences are somehow due to vicissitudes of preservation or other factors and that these size ranges are unreliable. However, samples of the Upper Stromness beds, Sandwick fish bed, Upper Rousay beds, and Eday flags (all from the Orkneys) have yielded spores of this type and the size of spores is much greater in the lower two beds than in the upper two.



TEXT-FIG. 12. Frequency distribution graph to show the spine length of *Ancyrospora ancyrea* (Eisenack) comb. nov. and *A. longispinosa* sp. nov. Based on 100 specimens of *A. ancyrea* from each sample.

Text-figs. 12, 13 show the decrease in spine size and the increase in the 'body'/spore diameter ratio in the Upper Rousay sample. However, these three graphs only show the variation of one or two characters whereas in separating the varieties there are three main characters involved. In order to obtain a more accurate picture of the assemblages the spores have been divided into a series of arbitrary types (see Table 1).

The results tabulated above show a difference between the two 'populations'. To determine whether this difference is real or apparent the table was treated as a $2 \times n$ contingency table. Table 1, however, had to be slightly modified as the expected frequency in some of the cells is below 5. This was done by grouping medium and long spines together (Table 2). The latter was subjected to a χ^2 test from which a value of $\chi^2 = 144{\cdot}12$ was obtained. This shows that the two 'populations' can clearly be distinguished by the proportions of morphotypes that each contains and that it is extremely unlikely that the differences are due to chance.

The characters spine length and 'body'/spore diameter ratio appear to be related; they have been tabulated (Table 3) and subjected to a χ^2 test. The result shows there is a significant association between the two variables.

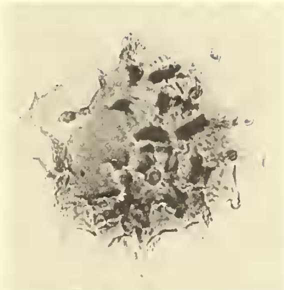
Thus from the above considerations it seems that there are real differences between the two 'populations'.

EXPLANATION OF PLATE 27

All magnifications $\times 300$.

Figs. 1–2. *Ancyrospora ancyrea* var. *spinobaculata* var. nov. 1, Specimen showing spines of variable width and length. Coal Heugh shales. 2, Large specimen, Basal beds, Easter Town burn.

Figs. 3–5. *Ancyrospora grandispinosa* Richardson 1960. 3, Specimen showing large 'central body', closely similar to G1 of Lang (1925). 4, Microtome transverse section showing solid flange and thick nature of the exoexine and 'body' membranes. 5, Broken specimen showing 'central body'.



1

2

3

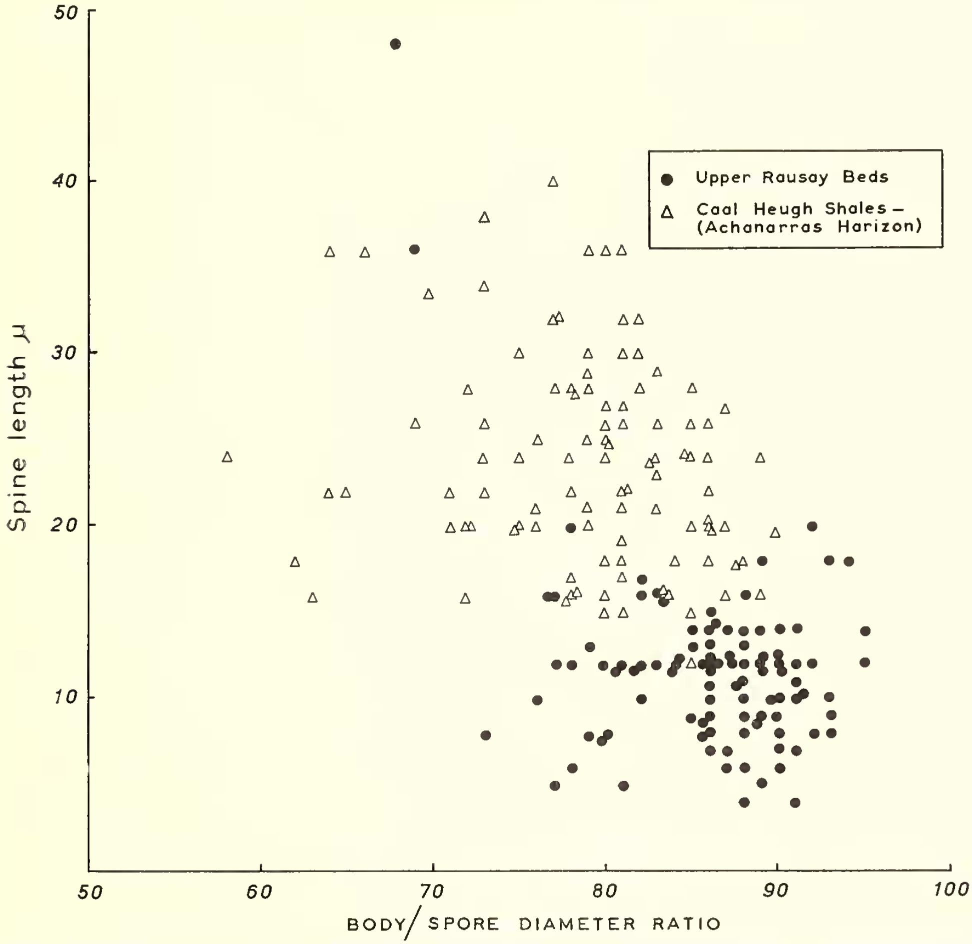
4

5

RICHARDSON, *Ancyrospora*

Variation in other samples

The Sandwick and Achanarras fish beds (Caithness and Orkney) and beds below the Achanarras horizon, which include the Lower Stromness beds (Orkney) and Basal beds (Easter Town burn), have also been examined. Unfortunately only the latter sample



TEXT-FIG. 13. Scatter diagram to show 'body'/spore diameter ratio plotted against spine length of *Ancyrospora ancyrea*. Based on 100 specimens from each sample.

yielded 100 measurable spores of *A. ancyrea*. The range of variation is very similar to that found in the Coal Heugh shales. There is, however, a greater number of forms with longer spines and with wide pseudoflanges in the Easter Town burn sample. In addition to *A. ancyrea* the species *A. longispinosa* sp. nov. is present in both the Lower Stromness beds (Orkney) and the Basal beds Easter Town burn (south of Moray Firth). Another form comparable in size and spine length (*H. ?corystus*) is found in the Lower Stromness beds, Sandwick and Achanarras fish beds.

In conclusion it is felt that the general trends in spore form described above are not due to factors of preservation or maceration. These trends can be seen throughout the sediments of the Orcadian basin although a variety of lithological types has been treated and the maceration technique standardized.

Stratigraphic applications of variation. Spores which probably belong to the genus *Ancyrospora* have been reported from Middle and Upper Devonian strata of Canada

'BODY'/SPORE DIAMETER RATIO

Category / Horizon	(50–70%)		(70–85%)			(85–100%)			Totals
	SPINE LENGTH								
	Long (25–50μ)	Medium (15–25μ)	Long	Medium	Short (0–15μ)	Long	Medium	Short	
Upper Rousay beds	1	0	0	7	21	0	5	66	100
Coal Heugh shales	3	5	30	38	0	5	17	2	100
Totals	4	5	30	45	21	5	22	68	200

TABLE 1. $2 \times n$ contingency table. Arbitrary division of the species *A. ancyrea* compared at two horizons.

'BODY'/SPORE DIAMETER RATIO

Category / Horizon	(50–70%)	(70–85%)		(85–100%)		Totals
	SPINE LENGTH					
	Medium (15– Long 50μ)	Medium Long	Short (0–15μ)	Medium Long	Short	
Upper Rousay beds	(a) 2	(b) 7	(c) 21	(d) 5	(e) 65	100 (n)
Coal Heugh shales	(A) 8	(B) 68	(C) 0	(D) 22	(E) 2	100 (N)
Totals	10	75	21	27	67	200
$g = \frac{a^2}{a+A}$ etc.	0·4	0·65	21	0·92	63·06	$\Sigma g = 86·03$
Calculated $\chi^2 = 144·12$; χ^2 from tables for 4 degrees of freedom = 18·467; P much $< 0·001$						

TABLE 2. $2 \times n$ contingency table. Arbitrary divisions of the species *A. ancyrea* compared at two horizons.

(Quebec and Alberta), Spitsbergen, Baltic Germany, and the U.S.S.R. (Belorussiya, Russian platform, and Bashkir, south-west Urals). The only statistical information available regarding these occurrences is their size range and in many cases these ranges are based on few observations. This data has been plotted along with the size distribution of the Orcadian spores (text-fig. 11). Although comparisons of this sort are of limited